absorption spectra only indicate the component parts of a compound so long as the colour of a given substance is characteristic of its chemical composition.

We notice an interesting discussion which arose at the last meeting of the Russian Society of Hygiene. M. Malarevsky, pointing out the yearly increasing myopy of scholars, proposed to print books with white letters on a black field, and proved the superiority of this system by experiments he has made with fifty scholars, as well as by experiments on the facility of discernment of black drawings on a white field and of white drawings on a black field, these last always being better seen from a greater distance than the former.

We have received a very full Catalogue of Official Reports upon Geological Surveys of the United States and Territories and of British North America, by Mr. F. Prime, assistant-geologist of Pennsylvania. It seems to be an enlarged continuation of the Catalogue by Prof. O. C. Marsh, published in the *American Journal* for 1867. The present list covers 50 pp.

At the last session of the U.S. Congress an appropriation of 250,000 dols. was made for the construction of a fire-proof building for the reception of such collections belonging to the National Museum as cannot be at present accommodated in the Smithsonian Building; and as the plans have already been prepared, it is understood that the work will be begun without delay. The design contemplates a building 301 feet square, with certain projecting corners, the whole covering a space of about 97,000 square feet. Although not quite equal to the area of the Government Building at the Centennial, it is capable of containing a much larger mass of material. The general plan is that of a pavilion, of one story, with brick walls and iron roof, the floor to be of concrete. The corner buildings or projections constitute offices connected with the administration of the Museum, to include a library room, a small lecture-room, and others. It is expected that the entire edifice will be completed and ready for occupation by April 1, 1880.

The whale whose bones have been so long exposed in the court-yard of the Jardin des Plantes at Paris, is to be demolished in compliance with a report from M. Quatrefages, who shows that the original number of vertebræ has been enlarged, and a series of important alterations have been successively made.

The publishing office of *Science News*, hitherto published at Salem, Mass., will shortly be removed to New York.

Many of our readers might like to know of Dr. Karl Möbius' address on March 5 last, on his assumption of the rectorship of the University of Kiel. Its subject is the passage from Goethe—"Leben ist die schönste Erfindung der Natur, und der Tod ist ihr Kunstgriff viel Leben zu haben."

The Second Annual Report of the Board of Trustees of the Western Pennsylvania Institution for the Instruction of the Deaf and Dumb is one of great interest, and we are sure would be perused with pleasure and profit by all who are interested in the important subject. The Institution seems to be conducted on thoroughly scientific principles, and its success seems very marked. The Report is published by Stevenson, Foster, and Co., Pittsburgh.

We have received a cheap edition of "The Caves of South Devon and their Teachings," by Mr. J. E. Howard, F.R.S., in which he endeavours to combat the long chronology assigned to the human race by Mr. Pengelly and others. Hardwicke and Bogue are the publishers.

The *North British Daily Mail* of March 29 contains reports of recent meetings of the Geological and Natural History Societies of Glasgow. In the former Mr. Young gave a descriptive notice of an interesting specimen of *Elephas primigenius* discovered about four years ago when sinking a pit-shaft on Mainbill Farm, near Baillieston, east of Glasgow. In the latter Mr. Harvie-Brown read a paper on the Mammalia of the Outer Hebrides.

"New Views in Astronomy, illustrated by Working Models and Diagrams, and Demonstrated by Inductive Philosophy," is the title of a quarto pamphlet by Mr. John Harris, published by Wertheimer, Lea, and Co., of Finsbury Circus.

The additions to the Zoological Society's Gardens during the past week include a Yak (*Bison grunniens*) from Bhootan, presented by the Hon. Ashley Eden, K.C.S.I.; a Japanese Goat Antelope (*Capricornis crispus*) from Japan, presented by Mr. H. Pryer, C.M.Z.S.; a Rhesus Monkey (*Macacus erythræus*) from India, presented by Mr. J. Roberts; a Grivet Monkey (*Cercopithecus griseo-viridis*) from West Africa, presented by Mr. W. B. Greenfield; a Common Seal (*Phoca vitulina*), British Isles, presented by Capt. Chas. Rawle; a Red-throated Diver (*Colymbus septentrionalis*), British Isles, presented by Mr. J. S. Thompson; a Masked Parrakeet (*Pyrrhulopsis personata*) from Fiji, an Entellus Monkey (*Semnopithecus entellus*), from India, deposited.

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# *THE RESULTS OF RECENT RESEARCHES IN ANIMAL ELECTRICITY*[1]

## I.—INTRODUCTORY OBSERVATIONS

### *The State of the Subject Ten Years Ago*

UNTIL the year 1867 certain theoretical conceptions based upon the classical investigations of du Bois-Reymond prevailed in the whole department of animal electricity. It may indeed be said that du Bois-Reymond created this branch of modern physiology, for it was he who first struck out the modern method of research and gave the lead to recent investigation. To his individual labours we owe not only the establishment and the orderly arrangement of many facts which had been left ill-defined by his predecessors, but also the actual discovery of a still greater number of fundamental value. These fundamental facts, briefly summarised, were the following:—

1. Muscular fibres and nerve-fibres when cut across exhibit a current directed within them from the transverse to the longitudinal surface, the electromotive force of which may equal one-twelfth of a Daniell's cell.

2. The negative potential of the transverse section also belongs, though in a less degree, to the natural terminations of the fibres of muscle ("natural transverse section"); but in this case it may be wanting, or even be changed to a positive potential. This diminution, absence, or reversal, of the common condition, to which the term "parelectronomic state" is applied, would seem to be favoured by the continued action of cold.

3. If a certain portion of a nerve-fibre be traversed by a galvanic current, the remaining portions, or the extra-polar regions, become the seat of an electromotive force which has the same direction as the traversing current, and which is strongest in the vicinity of the poles (electrotonus). This influence extends only so far as the structural integrity of the fibre is complete.

4. Muscles and nerves with artificial transverse sections exhibit during the period of stimulation a diminution ("negative variation") of their proper current. In uncut muscle the negative value of the diminution or variation becomes algebraically added to whatever current may be already present in the natural termination of the muscle.

Upon these facts du Bois-Reymond had based the following theory:—

1. Muscle- and nerve-fibres contain electromotive molecules suspended in an indifferent conductor, which present positive surfaces to the longitudinal surface or section, and negative surfaces to the transverse surface or section.

2. At the natural terminations of the muscular fibres are arranged particles of a peculiar kind, the presence of which is

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[1] A lecture delivered on February 2, 1878, before the Medical Society of Zurich, by Dr. L. Hermann, Professor of Physiology in the University of Zurich, and published in the "Vierteljahrsschrift d. naturf. Ges. in Zurich," 1878. All the papers referred to in this lecture which have no author's name attached are papers of the author himself.

more or less marked, and which present positive instead of negative surfaces towards the ends of the fibres. Cold, according to the theory, favours the development of this "parelectronomic layer."

3. The electrical molecules of a nerve, under the influence of a current which traverses it, assume a new arrangement which consists in their turning negative surfaces towards the positive pole and positive surfaces towards the negative pole. If we conceive these molecules as electrically dipolar in the state of rest, they would be arranged in inseparable pairs, the positive pole of each member of a pair being turned to the positive pole of the other, the negative surfaces of the molecules being all turned to the transverse sections; and the action of the current would consist in an arrangement of all the molecules in the form of a pile. As this rearrangement of the molecules extends in a less degree beyond the portion of nerve traversed by the current, electrotonic forces are developed.

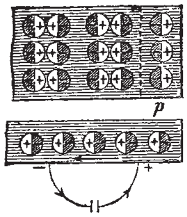

Fig. 1.

In Fig. 1 the upper diagram represents the normal, the lower the electrotonic, arrangement of molecules; above *p* are seen the parelectronomic molecules of the natural termination of the fibres.

4. During stimulation either the electromotive forces of the molecules diminish, or the latter assume a new arrangement, in which they appear less active externally; but the parelectronomic molecules take no share in these changes.

The promulgation of this molecular theory aroused many expectations. It appeared probable that the essence of the condition of activity and of its conduction in muscle and nerve was connected with the electrical properties of certain particles, rotation, oscillation or some other change in one particle leading to similar changes in neighbouring particles. Moreover, it appeared conceivable that even the contraction of muscle might be explicable by the actions of attraction and repulsion among the same particles.

Although speculation upon the origin of these electro-motive forces in muscle and nerve had hardly taken shape, and although the founder of the molecular theory observed a praiseworthy reserve in regard to all such speculation, yet up to the year 1867 it was pretty generally, if tacitly, assumed that the chemical processes occurring in muscles and nerves at rest were essential to the maintenance of the electromotive molecules in constant activity. In a similar way it was taken for granted that excitation depended ultimately upon certain movements of the electromotive molecules which were, of course, associated in some manner or other with increased consumption of oxygen and increased oxidation.

### *Researches which called forth New Views*

Researches which I made upon the exchanges of the gases and other constituents of muscle[1] furnished me with results which differed materially from the then prevailing conceptions of the functional processes occurring in these organs. I found that muscles contain no oxygen capable of being yielded to a vacuum, and nevertheless that they are capable of prolonged exertion in a medium entirely free from oxygen; hence I concluded that the chemical process which underlies muscular work is not a process of oxidation, but a process of decomposition, in which, by the saturation of stronger affinities through the passage of atoms into more stable atomic combinations, energy is set free, just as in the alcoholic fermentation of sugar.[2]

Amongst the products of this decomposition in muscle there occurs carbonic acid. A comparison of the quantities of carbonic acid set free during muscular exertion, and during muscular rigor, showed that in both cases the carbonic acid must spring from the same source, and thus, with the help of an analogous result to which J. Ranke had arrived in the case of lactic acid, a complete analogy between the chemical processes of *contraction* and of *rigor*, was found to hold good. Both processes are processes of decomposition, and as products of the decomposition are known carbonic acid, lactic acid, and in the case of rigor an albuminous coagulum discovered by Brücke and Kühne, which may perhaps in the future be ascertained to be a transitory phenomenon even in the case of contraction. The absorption of oxygen by muscle has nothing to do with this process of decomposition; the former is related to a synthetical process of restitution in which certain of the products of decomposition are perhaps again utilised. In this way was explained the independence (in point of time) between the absorption of oxygen and the production of carbonic acid by muscle.

According to this conception there occurs, during the condition of rest, a perpetual but slow decomposition and a slow process of restitution; the latter is dependent upon a supply of blood containing oxygen. If the supply be intercepted, then the whole store of decomposable matter within the muscle becomes exhausted, and the muscle passes into rigor. During contraction the process of decomposition is suddenly quickened, and the process of restitution can barely keep pace with it: when the latter lags behind the former *fatigue* results.

The analogy between contraction and rigor had attracted attention long before, although, excepting the shortening of muscle, no other feature common to the two processes was known. Rigor had been designated as the last contraction of dying muscle. The new conception reversed the comparison, inasmuch as it assimilated contraction to a momentaneous and transitory rigor; and, since then, the physical analogies between contraction and rigor have been discovered to be more and more numerous. It has been found that in rigor as well as in contraction the volume of the muscle diminishes somewhat, and that in both processes heat is developed; while, to complete the relationship, it has been lately observed that certain evident transitional stages occur between the two.[1] Thus stimuli of excessive intensity, when applied to muscle, lead to a condition in which the state of contraction never perfectly disappears, but leaves behind it a residue of shortening. Fatigue and the process of death favour this condition of persistent, rigor-like contraction (Schiff's "Idiomuscular Contraction"), and a similar condition is induced by many muscular poisons, as veratria, delphinia, digitalin, emetin, caffein, &c.

While pursuing the analogies between the conditions of contraction and rigor I came upon a view of the nature of animal electricity which differed essentially from that which was then in existence.[2]

### *Fundamental Conceptions of the New Theory*

The most important and at that time the most certainly ascertained fact was this, that a transversely divided muscular fibre exhibits, until it has become completely rigid, a negative potential in the plane of the section, and that this difference of potential diminishes or disappears during the state of functional activity. Having regard to the chemical and physical analogy between the processes of activity and of rigor; and considering the fact that when an artificial cross-section is made there is from the very first a portion of matter within the fibre which is passing into rigor, I explained this phenomenon on the assumption that the process of rigor, like the process of contraction, so modifies the protoplasm that it takes on a lower potential than the unchanged inactive protoplasm.

If this be so then an artifical cross-section must preserve a lower potential so long as the fibre has not become rigid throughout its entire extent, and on stimulation of the portion yet alive a diminution of the electrical difference must result.

## II.—The Electrical Currents of Organs at Rest

### *The Absence of Currents in Muscles which are at Rest and Uninjured*

In order to sustain the new theory of animal electricity (which, in opposition to the "Pre-existence Theory" of du Bois-Reymond I have designated the "Alteration Theory"), it was in the first place necessary to determine whether absolutely uninjured muscles are the seat of a muscular current.

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[1] Untersuchungen über den Stoffwechsel der Muskeln ausgehend vom Gaswechsel derselben. Berlin, 1867.

[2] Similar views have been more recently expressed, and with a somewhat more general application, by J. Liebig, in the "Sitzungsber. der bayr. Acad.," 1869. ii. 4; and by Pflüger, "Arch. f. d. ges. Physiol.," x. p. 251, 1875. I myself had extended this view to the chemical processes in nerves and glands.

[1] "Arch. f. d. ges. Physiol.," xiii. p. 371, 1876; xvi. p. 252, 1878.

[2] "Untersuchungen zur Physiologie der Muskeln und Nerven," 2 u. 3 Heft. Berlin: 1867, 1868.

Muscles cut out of the body possess almost invariably imperceptible injuries of a mechanical or chemical nature. In the first researches of du Bois-Reymond the muscles were regularly moistened with saturated solutions of common salt, and thereby, to a certain extent, corroded. Hence he was led to ascribe to the natural terminations of muscular fibres the negative potential which is exhibited by artificial transverse sections. This source of error was indeed discovered by du Bois-Reymond himself; but, after he had removed it, there yet remained other electrical phenomena apparently dependent upon the terminations of the fibres, differing, however, entirely from that just mentioned and obeying no strict rule in respect of direction of current. For these phenomena the hypothesis of the parelectronomic layer was introduced.

The more, however, all injuries are avoided in the preparation of muscles about to be used for such observations, the nearer is the approach to complete absence of currents. Chief among the injuries in the case of the frog is that produced by contact with the caustic secretion of the external skin.[1] The gastrocnemius is a muscle which may very readily be defended from such contact during its preparation, and it then exhibits merely weak currents of indefinite direction, such as are found in all circuits containing moist conductors.[2] The muscles of the thigh are, without exception, so connected with one another or with neighbouring parts (skin, bones, &c.) that they cannot be prepared without sustaining *mechanical* injuries in the course of the necessary manipulation.[3]

The statement that cold favours the development of a currentless condition, or of opposing currents, in muscle is not confirmed. The gastrocnemii of freshly-caught frogs do not differ electrically from those of frogs kept for a long time previously in an ice-cellar.[4] It is perhaps as well to observe that muscles which have been actually frozen suffer injury in the subsequent process of thawing, and are therefore to be avoided in these researches.

The most promising method of testing perfectly uninjured muscles appeared to be to examine them in the unskinned animal. Du Bois-Reymond,[5] who was the first to hit upon this method of observation, encountered an unexpected difficulty in the cutaneous currents which almost all animals possess. If it is first attempted to abolish the cutaneous currents by cauterising the skin with salt solutions, the solution rapidly penetrates the skin and attacks the underlying muscles; this is observed to occur by the gradual development of the same current as is induced when the naked muscle is moistened by caustic agents. That the muscles have already been attacked by the time the muscular current is developed[6] may be directly shown by employing silver-nitrate as the cauterising solution, when its action upon the tissues subjacent to the skin is manifested by rendering them opalescent.[7] If the skin is cauterised in places beneath which there are no aponeurotic muscular surfaces, no muscular current can be discovered, or at the most only such weak and irregular currents as count for nothing in the case of a circuit formed of moist conductors; not even the action of caustics, nor abrasion renders the skin absolutely currentless.[8]

Fishes possess no cutaneous current; in their case it suffices to connect any two points on the surface of the skin with the galvanometer in order to ascertain the absence of a muscular current.[9] These animals, like the frogs used in these experiments, must be rendered motionless by the action of curare.

According to the recent researches of Engelmann the heart offers an example in which it is easy to demonstrate the absence of a muscular current.[10] To do so it is merely necessary to remove the pericardium, an operation which can be performed without inflicting any injury upon the muscular substance. The heart is currentless, but every injured spot in it possesses a negative electric potential in reference to the rest. The pre-existence theory can only explain this fact, and the previously mentioned fact of the want of a current in the fish, by the most improbable surmise made expressly to suit the cases, that no muscular fibre has its termination directed towards the surface.

### *No Electromotive Force pre-existent in Muscle*

Another method of deciding whether a current pre-exists in muscle appeared to be to determine whether, immediately after a transverse section is made, the current is present in full force, or whether an interval, however short, is required for the development of it. Were the latter the case it would be impossible for the doctrine to be correct which assumes that electromotive molecules exist ready formed in muscle and are merely laid bare by the knife. The experiments,[1] which were made by me in the years 1875 to 1877, to decide this question, have settled it in opposition to the pre-existence theory. With the help of a special apparatus the galvanometer circuit was closed at the moment when an injury was inflicted upon a previously uninjured muscle and then opened again after a very minute interval of time. The deviation observed was smaller than in a second trial made after the muscular current had already been developed, and in which the current was allowed to act on the galvanometer for the same period of time. The muscular current, therefore, requires time for its development: it does not pre-exist.

### *The Currents of Nerves, of Glands containing Blood, of Plants, &c.*

It was to be surmised that other protoplasmic tissues than muscle would exhibit the phenomenon that portions of the tissue which are in process of dying have a lower potential than the yet living parts. First in importance in this respect is nerve: the current of nerve was discovered by du Bois-Reymond, and, like that of muscle, explained by a molecular hypothesis. Uninjured terminations of nerves are, for many reasons, not available for electrical researches; nevertheless, on the ground of the analogy to muscles, no one doubted the existence of a current in nerves, nor the applicability to them of the molecular scheme. With the discovery of the absence of a current in uninjured muscles, however, the analogy cuts the other way.[2] Henceforward there was not the slightest ground to assume the existence of a current in nerves at rest, except that developed by artificial sections. We shall see that even the phenomena of electrotonus do not in the least justify the molecular hypothesis.

Besides nerves, two other groups of protoplasmic apparatus have been examined by myself; and it has been found that in them, also, artificial sections possess a negative potential when compared with the rest of the organs. In the cases of both groups it afterwards appeared that the observations had previously been made by others. The first case was that of the glandular organs of the frog,[3] in which Matteucci had already found artificial cross-sections to be negative. I made out that this character is only present when the vessels contain uncoagulated blood, to the changes in which at the exposed surface it seems the electromotive force is due. The second case was that of the negative potential of artificial cuts and of cauterised spots in plants,[4] facts first observed by H. Buff.[5] Both phenomena are of such a kind that it is absolutely inconceivable to apply a molecular theory to them; yet notwithstanding the attempt has been seriously made.

### *The Dependence of Currents upon the Contact of Normal and Injured Protoplasmic Tissue*

When examining the artificial cross-sections of plants I observed that the lower potential of the exposed surface quickly disappeared, but that a new section soon restored the original condition. I explained this behaviour by supposing that, according to the fundamental law, the lower potential of the cross-section only persists so long as the cells which are implicated in the section possess a remnant of living protoplasm. If the cells are entirely dead, the current must cease. In this manner we can explain why, in plants with obviously long fibres, artificial longitudinal sections have a higher potential than artificial transverse sections;[6] for the cells which are split up lengthwise die much more rapidly than those which are cut across. The same transitory character of the current which I have discovered in artificial cross-sections through vegetable tissues has lately been observed by Engelmann[7] in the case of the heart and of organs possessed of unstriped muscular fibres, and has been similarly explained. These organs are composed of independent cellular elements placed one behind the other in rows, and the current of one section can therefore only last until the injured cells have died from end to end.[1] In the last place the same phenomenon was discovered, in the case of nerves, by Engelmann. Here the nodes of Ranvier constitute cellular boundaries which effectually confine the process of death[2] to the internode immediately injured during section, although they offer no greater barrier to the transmission of the excitatory condition than do the cell-boundaries in the heart, intestines, or uterus.[3]

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[1] "Arch. f. d. ges. Physiol.," iii. p. 37, 1870.
[2] *Ibid.*, p. 16, 35. [3] *Ibid.*, xv. p. 227, 1877. [4] *Ibid.*, xv. p. 226, 1877.
[5] Du Bois-Reymond, "Untersuchungen über thier. Electr.," ii. 2 Abth. p. 7.
[6] "Untersuchungen," Heft iii. p. 6, 1868. [7] *Ibid.*, p. 14.
[8] *Ibid.*, p. 14; "Arch. f. d. ges. Physiol.," iii. pp. 16, 23, 26, *et seq.*; iv. p. 149, 1871.
[9] "Arch. f. d. ges. Physiol.," iv. p. 152, 1871.
[10] Engelmann, "Utrecht'sche physiol. Onderzoek." (3), iii. p. 82, 1874.

[1] "Arch. f. d. ges. Physiol.,' xv., p. 191, 1877.
[2] "Untersuchungen," Heft iii., p. 25, 1868. [3] *Ibid.*, p. 88.
[4] "Arch. f. d. ges. Physiol.," iv. p. 155, 1871.
[5] Buff, "Ann. d. Chemie," lxxxix. p. 76, 1854.
[6] "Arch. f. d. ges. Physiol.," iv. pp. 159, 163, 1871.
[7] Engelmann, "Arch. f. d. ges. Physiol.," xv. p. 116, 1877.

### *Disappearance of Demarcation Currents (Demarcations-ströme) under the Influence of the Natural Reparative Processes of the Body*

It was reserved for Engelmann to discover yet another fact opposed to the doctrine of the pre-existence of electrical forces in muscle.[4] If in a living frog a muscle be divided subcutaneously the negative potential of the artificial section diminishes continually, and ultimately disappears, under the influence of the blood circulating in the part and of the nerves supplying it. As, therefore, nature tends to render artificial sections currentless, it is clear that in the natural condition no muscle can be the seat of currents, but every muscular current observed during rest must spring from injuries.

Inasmuch as all currents exhibited by muscles and nerves in a condition of inactivity (except those caused by inequalities of temperature or by the passage of extraneous currents) depend upon the contact of dying and living matter, and since the electromotive force has its origin in the surfaces which form the boundary between the two, I have called these currents of rest "demarcation currents" (Demarcations-ströme).

### *Influence of Temperature*

If the muscular substance within the same fibre exhibits differences of temperature the warmer spots possess[5] a higher potential than the colder, so long as the temperature does not attain the limits of heat-rigor, and the consequent negative potential ensue. In exactly the same degree as living substance acquires through heat a higher potential than other living substance, is its potential exalted as regards dying substance. Hence, it is not merely that the demarcation-current becomes more powerful by heating the whole muscle, as was in part revealed to du Bois-Reymond, and recently established by Steiner in regard to nerves, but the force of the demarcation-current is dependent only on the temperature of the living substance at the point of application of one galvanometer-electrode, and not on the temperature of the substance lying between the poles. In a word, portions of muscular substance in different conditions form together a voltaic series.[6]

### *The Currents of Entire Muscles*

As has been already remarked, wholly uninjured muscular fibres possess no current. All currents of muscles at rest are, therefore, variations in temperature excepted, the results of injuries. The properties of the current are most simple in the case of a muscle with parallel fibres, and cut transversely at right angles. In this case all the boundary surfaces between dying and living tissue are parallel to the section, and every point in the transverse surface has a lower potential than any point in the longitudinal surface.[1] As, however, the muscle possesses between its fibres and on its surface indifferent conducting tissues through which the demarcation-currents can in great part become equalised—such tissues as sarcolemma, perimysium, the dead tissue of the cross-section—two important results follow. In the first place the force of the currents obtained by applying the galvanometer poles to two spots of different potential represents but a fraction of the electromotive force of a single fibre. In the second place the positive potential of the longitudinal surface and the negative potential of the transverse surface are so distributed as to be most marked at the centre of the respective surfaces. Hence arise the so-called "weak currents" when the galvanometer poles are applied to unsymmetrical points on the transverse or longitudinal surface.[2] But the weak currents of longitudinal surfaces may, especially in nerves, be in part due to an electrotonic extension of the demarcation-current which will be the subject of discussion later on.

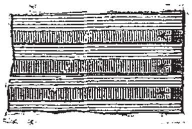

FIG. 2.

In oblique sections there occurs a peculiar arrangement of the level-lines[3] (Niveau-linien), inasmuch as there intervenes an electromotive force which is directed from the acute to the obtuse edge of the slanting section: such currents are called "currents of inclination." Du Bois-Reymond explains this force by the step-like arrangement which the terminal molecules form in the slanting section; but it is clear that the same mode of explanation is just as well adapted to the step-like arrangement of the boundary-surfaces between dying and living tissue in the successive sets of fibres (Fig. 3).

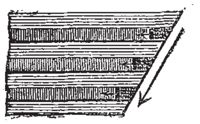

FIG. 3.

The molecular theory, therefore, is not needed to explain the currents of inclination of a *bundle* of fibres; it would only be indispensable in the case of a current of inclination of a *single* obliquely-cut fibre, did such a fibre possess one; but this is precisely what no one has demonstrated or can demonstrate. The circumstance that many muscular fibres present slanting facettes at their terminations in tendons[4] offers no opportunity to support the molecular theory; for such tendons possess no current of inclination in the uninjured condition, while, in the injured condition, the tissue of each fibre invariably dies down to a surface at right angles to the long axis of the fibre, and thus the conditions for the current of inclination arise (Fig. 3).

In all cases of partial injuries to muscle it is only the injured fibres which are the seat of electromotive action; the remainder merely form indifferent conductors which give facilities for local equilibrations. The weak currents of such muscles have, therefore, no regular relation to the surface of the muscle, as all depends upon the situation of the injuries: hence the irregular currents of so-called parelectronomic muscles.

When injuries, of whatever kind, affect the whole surface of a muscle, the probability is that a current will be detected in the muscle flowing from one end of it towards the longitudinal surface; and, in fact, when tested, this is found to be almost always the case. If a slight injury has been inflicted upon the lateral surface of a muscle the death-changes in fibres which have been opened longitudinally will speedily be checked at the boundary of the next fibre, while the death-changes which have been started at the ends or cross-sections will creep along the whole length of the fibres and occasion a lasting current. This has been previously alluded to, when the transitional nature of the demarcation-current in the heart, intestines, &c., was explained.

Local injuries to the external surface of a muscle give rise to local currents; but these currents, when a conductor is stretched from the longitudinal to the transverse surface, produce hardly any effect; whilst the demarcation-currents at the dying end of the muscle are under very favourable conditions for conduction, and

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[1] I made an exactly similar observation in the spring of 1877 on the tissues of young Medusæ which were sent to me through the kindness of Prof. Hensen, of Kiel.

[2] Engelmann, "Arch. f. d. ges. Physiol, xiii., p. 474, 1876.

[3] Gad und Tschiriew ("Verhandl. d. physiol. Ges. zu Berlin," 1877, Nr. 21) deduce the disappearance of the current in nerves from the fact that, after the death of the divided internodes the seat of electromotive force, viz., the ends of the internodes of the next row are no longer in one transverse plane, whence the resulting current is much diminished by partial equalisations. The value of this observation is obvious when it is remembered that the length of the internodes of Ranvier is, generally speaking, only 1—1½ mm.

[4] Engelmann, "Arch. f. d. ges. Physiol.," xv., p. 328, 1877.

[5] "Arch. f. d. ges. Physiol.," iv. p. 163, 1871.

[6] *Ibid.*, p. 178.

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[1] The best method of applying the electrode to an artificial transverse section of muscle; so as to avoid any abduction of current from the living portion, is to produce a heat-rigor of the end of the muscle, and to apply the electrode to the rigid part ("thermal cross-section"); cf. "Arch. f. d. ges. Physiol.," iv. p. 167, 1871.

[2] Du Bois-Reymond, "Untersuchungen," i. 1848.

[3] Du Bois-Reymond, "Arch. f. Anat. u. Physiol.," 1863, p. 521; "Monatsber. d. Berliner Acad.," 1866, p. 387.

[4] Du Bois-Reymond, "Monatsber. d. Berliner Acad.," 1872, p. 791.

the forces of the local currents are, on account of the usual oblique application of the muscular fibres to their tendons, generally summed into currents of inclination.

### III.—ELECTROTONUS

#### *Considerations opposed to the Molecular Theory of Electronus*

The explanation adduced in the Introductory Remarks, in order to elucidate the electrotonic condition of nerves has many theoretical difficulties which cannot be here entered upon. The theory appears, however, to be amenable to an experimental proof. If, namely, the molecules of the portion of a nerve traversed by a current arrange themselves in the direction of the current, the electromotive force of the current should receive a very appreciable increase; or, in other words, the current should become very much greater when it passes through a piece of living nerve than when it traverses a dead piece of similar dimensions. On trying this experiment, however, I find no such difference; or the differences found are far from agreeing with the molecular theory.[1]

#### *Electrotonic Phenomena observed in Conductors with Polarisable Cores*

An experiment of Matteucci's[2] gave the clue to an explanation of electrotonic phenomena. He found that a metallic wire which is surrounded by a moist envelope exhibits currents possessing the characters of the electrotonic currents of nerves, whenever a galvanic current is passed, at any point, through the moist envelope. Matteucci discovered, in addition, that the currents cease when the wire is of amalgamated zinc and the envelope is moistened by a saturated solution of zinc sulphate. Hence it follows that the phenomenon depends upon a polarisation between the core and the fluid.

I examined the phenomenon more closely,[3] passing metallic wires through a glass tube filled with fluid and possessing lateral processes for the conduction of currents, and my experiments confirm the fact that electrotonic currents only occur when a polarisable core is present. Further, it was seen that the currents only extended so far as both core and envelope possessed unbroken continuity, whereas continuous contact of the two was not necessary. Lastly, I determined the laws regulating the time of development of these currents, their duration, their cessation on opening, their dependence upon the distance, and the length of the portion of core traversed by the polarising current, their combination and superposition, &c. All the phenomena may be grouped without difficulty under a simple theory.

As the current *a* E *k* (Fig. 4) applied to the envelope endeavours to reach the core K K, it splits up, if no polarisation be present, in such a manner that only the conducting threads in the immediate neighbourhood of the electrodes are able to catch an appreciable branch of the current. If on the other hand polarisation occurs at the surface of the core, this surface opposes a considerable and evenly distributed resistance; and, as in relation to it, the resistance offered by the length of the conducting wires is small, the current, under the influence of polarisation, extends much further along the conductor than when no polarisation takes place. If a galvanometer-circuit is arranged as shown in the diagram (at G, G′, or G″) it receives an offset from the main current as if there existed in the region examined an electromotive force of like direction with that of the polarising current. This polarisational extension of the current only continues where both core and sheath are uninterrupted.

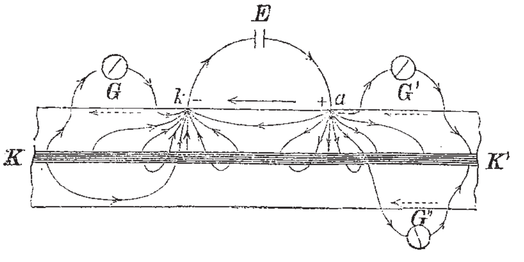

FIG. 4.

The abducted currents are at the same time, on mathematical grounds, a measure of the degree of polarisation at the points touched; and thus afford a means of tracing the extent of polarisation along the core. The curve representing the polarisational values at various points of the core—in general an exponential curve—has at the positive pole a positive maximum and a negative at the negative pole. In the region traversed by the current the curve cuts the axis at the so-called "indifferent point" (Fig. 5, *i*); and in the extra-polar regions it approaches the axes on both sides asymptotically. The curve is represented in Fig. 5, where, as a matter of subsequent convenience, the ordinates of positive polarisation are taken below the axis instead of above.

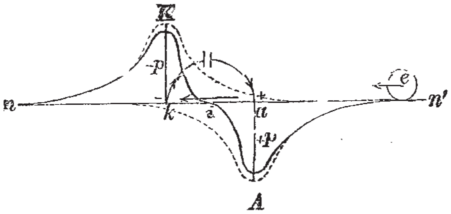

FIG. 5.

#### *Internal Transverse Polarisation of Muscles and Nerves*

In the year 1871 I discovered that the resistance offered by muscles and nerves to the passage of a current across their fibres was from five to nine times greater than the resistance offered by a current passing in direction of the fibres.[1] In the case of muscle this difference disappears almost entirely when rigor sets in; whilst in dead nerves it certainly persists, though reduced to one half. Further investigation of these facts disclosed their dependence upon a specific internal polarisability, which, in the case of muscle, is entirely associated with the living condition, and, in the case of nerve, in great part so associated. This fitness for polarisation by transversely-directed currents can only be due to a stratification of heterogeneous conductors across the tissue, which is wanting in its longitudinal axis. And since it is common to muscles and nerves, the stratification on which it depends must be sought in the typical structure which is common to the two organs, viz., the tubular nature of the fibres. We may assume, therefore, that polarisation takes place between the peculiar, active, substance of muscle- and nerve-fibres and the indifferent tissue ensheathing it.

#### *Explanation of the Electrotonus of Nerves*

As, accordingly, there exist in nerve-fibres all the essential conditions of the electrotonic extension of currents in conductors with polarisable nuclei, it may be assumed that the electrotonus of nerves is fully explained.[2] It is true that the core-substance of nerves is no better a conductor of electricity than the sheath-substance, while in the sheathed wire of Matteucci's experiment the core was of metal. But theory teaches that the electrotonic extension occurs even when the conducting powers of sheath and core are equal, if only polarisation takes place between the two.

This explanation of electrotonus, as I have shown in detail, completely covers all the phenomena. Especially does it account for the facts that the electrotonic state requires no appreciable time for its establishing;[3] and that it cannot extend past a ligatured spot. Whenever a nerve is crushed, the continuity of the core is broken, since, at the crushed spot, the core is killed and converted into indifferent tissue.

As muscle-fibres also possess polarisable cores, they must be endowed with electrotonic properties; nevertheless, neither du Bois-Reymond nor I at first succeeded in demonstrating them by galvanometric means; though, truly, just as little could their absence be distinctly affirmed. But theoretical considerations disclosed the reasons why muscle was less favourable to electrotonic phenomena than nerve;[4] and lately I have succeeded, by employing better contrivances, in demonstrating with the galvanometer the electrotonus of muscle.

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[1] "Untersuchungen," Heft iii. p. 67, 1868; "Arch. f. d. ges. Physiol.," vi. p. 328, 1872.

[2] Matteucci, *Comptes Rendus*, lvi. p. 760, 1863; lxv. pp. 151, 194, 884, 1867; lxvi. p. 580, 1868.

[3] "Arch. f. d. ges. Physiol.," v. p. 264, 1871; vi. p. 312, 1872; vii. p. 302, 1873.

[1] "Arch. f. d. ges. Physiol.," v., p. 223, 1871.

[2] *Ibid.*, vi. p. 328, 1872.

[3] "Helmholtz, "Monatsber. d. Berliner Acad.," p. 328, 1854; L. Hermann, "Arch. f. d. ges. Physiol.," viii. p. 272, 1874.

[4] "Arch. f. d. ges. Physiol.," vi. p. 350, 1872.

An important addition to our knowledge of the electrotonus of nerves will be discussed at length in the sequel.

## IV. The Electrical Currents of Organs in Activity.—A. Muscles

### *The Fall in Potential accompanying the Excitatory Wave*

After Helmholtz had proved in the case of nerves, and Aeby in the case of muscles, that excitation is transmitted along the fibres with a measurable velocity, J. Bernstein undertook to investigate the electrical processes associated with the transmission.[1] To do so, he employed an instrument of his own devising, by means of which he could discover the electrical conditions of a muscle at any period after stimulation. He found in muscle on direct stimulation that a zone or section of negative potential arose which travelled down the fibre from the stimulated point with the same velocity as the wave of contraction. This phenomenon was readily explained by the theory of du Bois-Reymond, according to which the molecules of excited tissue suffer a diminution of activity, whence all excited spots must be electrically negative in relation to the inactive parts of the organ. Accordingly the phenomenon was designated "undulatory propagation of the negative variation."

On the assumption already made that excited tissue has, like dying tissue, a lower potential than the unchanged tissue, the fact is also at once explained, and I have named the currents called into being by the contact of excited with resting tissue, "functional currents" (Actions ströme).[2]

### *The Phasic and the Tetanic Functional Current*

When a single excitatory wave runs over a muscular fibre which is connected at two points with the poles of a galvanometer, that point is of lower potential than the other beneath which the excitatory wave is passing at the time; or, if a wave happens to be passing both points at once, that point has the lower potential where the wave has the greater intensity or the stronger phase. Hence arises what may be called a "phasic functional current," the initial phase of which is a current proceeding *from* the stimulated spot, and the final phase a current in the opposite direction. The two phases are equal when the excitatory wave suffers no diminution in its course.

If a muscular fibre is tetanised, whether excitation travel in an undulatory form down the fibre or seize it as a whole, every galvanometer-pole applied to the muscle will be of higher or lower potential, according to the excitatory value of the points of application.

### *The Tetanic Functional Currents of Injured and Uninjured Muscles.*

The first observations of du Bois-Reymond related to the tetanic functional current of muscles with artificial cross-sections. In such muscles the tetanic functional current is opposed to the demarcation-current, and manifests its influence in a "negative variation or deflection" of the latter. Since I regard the functional current as due to living muscle approximating in a certain degree to the condition of dying muscle, I have denominated such functional currents as diminish a demarcation-current "levelling," or "equalising," currents (ausgleichende).

Subsequently du Bois-Reymond discovered that uninjured muscles also exhibit a tetanic functional current proceeding from the stimulated point towards the end of the muscle. In order to reconcile this with his theory it became necessary to assume that the parelectronomic layer at the extremity of the fibre took part either not at all, or but slightly, in excitation. Finally the latter alternative was adopted, and it proved to be nearer the truth; for it was discovered that the functional current of uninjured muscles is less powerful than that of muscles cut across.[3] In a word, in order to explain the functional current of uninjured muscle, it was found necessary to assume that the extremities of a muscular fibre are less concerned in excitation than the middle.

While du Bois-Reymond was thus confining the limited participation in excitation to the extremities of the fibre, or, in other words, was locating the origin of the functional current in the end of the fibre, it occurred to me that the excitatory wave in its course over a muscular fibre might diminish in intensity;[1] whence it would follow, according to what was said in the foregoing section, that in tetanus an electrode placed near the stimulated point would have a lower potential or be electrically negative, to an electrode more remote. The direction of the diminutional or decremental current so obtained would agree both with observed facts and du Bois-Reymond's theory; but its force, instead of residing in the end of the fibre, is equally distributed over the whole course of the excitatory wave.

### *The Diminution in Intensity of the Excitatory Wave in Excised Muscles*

Shortly after I had expressed my belief that the excitatory wave would be found to diminish in intensity in its passage down the muscle, Bernstein actually observed that it was so.[2] But du Bois-Reymond surmised that the phenomenon might be the result of the abnormal conditions of the experiment, and ought, in fact, to be attributed to the moribund state of the excised muscle; and in support of his surmise he stated that perfectly fresh muscle, on direct stimulation, exhibits no decremental functional current between any two points of its substance.[3] He persisted, therefore, in assigning the origin of the functional current to the parelectronomic layer. Moreover, he expressed a doubt whether, on stimulating a muscle through its nerve, excitation is propagated along the muscle in the form of undulations.

Meanwhile, in my own experiments I invariably detected the decrement of excitatory wave in excised muscles, a decrement, it need hardly be observed, which increased with the degree of exhaustion of the muscle.[4] Further, I hit upon the following proof that the force of the functional currents is evenly distributed over the whole fibre. If, while a muscle is being tetanised at one end, the points of application of the galvanometer electrodes be shifted in relation to one another and to the seat of stimulation, a functional current will invariably be discovered proceeding away from the stimulus; and the force of the current will be found to depend solely upon the interval between the galvanometer poles, irrespective of their position in relation to the end of the muscle.[5] The same observations may be made on a muscle which is tetanised through its nerve.[6] A functional current may always be abducted from the muscle, the force of which is exclusively determined by the respective distances of the abducting electrodes from the "nervous equator"[7] of the muscle.

The above experiments prove that excitation, even on nervous stimulation, proceeds in the form of a wave; that in excised muscles it always suffers a decrement; that the tetanic functional current is decremental in its nature; and that its origin is not restricted to the ends of the muscular fibres, but is distributed over the whole course of the excitatory wave.

### *The Phasic Functional Current developed on Stimulation through Nerve*

The first examination of the phasic functional current of a muscle which is excited through its nerve was made by S. Mayer, under the supervision of Prof. Bernstein;[8] in their researches the gastrocnemii of frogs were used. They made out that stimulation was followed by the development of two currents in succession, of which the first to appear was a descending current and the second an ascending current. If the gastrocnemius had been previously injured at its lower end, the second, or ascending, current was less pronounced.

These results were subsequently established by some experiments of du Bois-Reymond,[9] as well as by others which I made with a special non-repeating apparatus adapted to single stimuli.[10] Du Bois-Reymond explained the phasic current as due to the asynchronism of the two forces concurring to produce the functional current. These forces were assumed to be located in the two extremities of the muscular fibres and to be directed each to the correspondent end of the fibre, on which account they would of necessity overlap. The descending functional current belonging to the lower end was supposed to arise more quickly and to disappear earlier than the ascending current of the upper end; and hence the appearance of phases. Inasmuch as injury to one of the ends of a muscle (or in other words, removal of the parelectronomic layer), according to Du Bois-Reymond, intensifies the functional current proper to that end, it is clear that, when the inferior extremity is injured, the lower (descending) functional current obscures the upper.[1]

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[1] J. Bernstein, "Monatsber. d. Berliner Acad." 1867, p. 72; "Arch. f. d. ges. Physiol." i. p. 173, 1868; "Untersuchungen ü. den Erregungsvorgang, &c.," Heidelberg, 1871.

[2] "Untersuchugen," Heft iii. p. 61, 1868; "Arch. f. d. ges. Physiol." xvi. p. 193, 1877.

[3] Du Bois-Reymond, "Arch. f. Anat. u. Physiol.," 1873, p. 548.

[1] "Untersuchungen," Heft iii., p. 60, 1868.

[2] Bernstein, "Untersuchungen, &c.," p. 64, 1871.

[3] Du Bois-Reymond, "Arch. f. Anat. u. Physiol.," p. 369, 1876.

[4] "Arch. f. d. ges. Physiol.," xvi. p. 194, 1877.

[5] *Ibid.*, p. 217. [6] *Ibid.*, p. 229.

[7] Each constituent fibre of a muscle receives the motorial end-organ of a nerve-fibre. The motorial end organs of all the fibres are not absolutely in the same plane; and by the term "nervous equator" I have designated their *mean level* in a given muscle. The "nervous equator" is that equatorial section of a muscle in relation to which the distances of the various motorial plates, when algebraically summed, amount to nothing. See "Arch. f. d. ges. Physiol.," xvi. pp. 234, 414, 1878.

[8] S. Mayer, "Arch. f. Anat u. Physiol.," 1868, p. 655.

[9] Du Bois-Reymond, "Arch. f. Anat. u. Physiol.," 1873, p. 584.

[10] "Arch. f. d. ges. Physiol.," xv. p. 235, 1877.

My own explanation[2] is essentially different from du Bois-Reymond's. According to my views the muscle must exhibit a descending current when the excitatory wave is at the upper end of the muscle, and an ascending current when at the lower end. Hence it is not the first, but the second phase, which is proper to the lower end of the muscle. The former, as I have shown, pertains to the moment when the excitatory wave is in the neighbourhood of the upper electrode—a condition most advantageously secured, owing to the peculiar structure of the gastrocnemius, by placing the electrode so as to abduct a current from the mid point of the fibres rather than from their upper end.

According to this theory it is clear that the descending phase must precede the ascending: for every excitatory wave is started at the middle point of the muscular fibre where the nerve enters, and only reaches the ends of the fibres at a later period. If, however, the lower end of the fibre have suffered injury, the excitatory wave running towards the injured part will be powerless to cause a current, owing to the constant negative potential of the injured end, and hence the second, ascending phase comes to nothing.

The fitness of this explanation was placed beyond doubt by experiments on the phasic functional current of regularly-constructed muscles.[3] In such muscles there invariably appeared in each half first an atterminal and then an abterminal phase (Fig. 6). The atterminal phases in both halves (1 in Fig. 6) coincide in time, arising, as they both do, in the mid-point of the fibre at the starting of the excitatory wave; in other words, the middle point of the fibre becomes negative in comparison with either end.

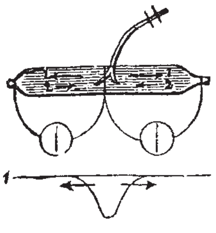

FIG. 6.

In like manner the abterminal phases of both halves coincide (2 in Fig. 6), being produced by the arrival of the excitatory waves at the extremities of the fibre: in other words, either end of the fibre becomes negative in comparison with the mid-point.

In this manner the wave-like propagation of the excitatory condition in muscle was established for the case of muscle stimulated through nerves, and, at the same time, another proof was afforded that the force of the functional current does not exclusively reside in the ends of the fibres.

Furthermore, it was directly shown in these experiments that the excitatory-wave in excised muscles, while traversing the fibres, experiences a diminution; for the second, abterminal phase was invariably much weaker than the atterminal, as is indicated in Fig. 6 by the length of the arrows and the height of the representative curve, and it invariably further diminished in the course of an experiment.

### *The Functional Current in wholly Uninjured Muscle in Man*

In the case of man the currents of normal resting muscle were secured from investigation by the obstacle of the skin. But Du Bois-Reymond found, during the violent voluntary contraction of the muscles of an arm or a leg, that the limb exhibited an ascending current. This he took to be the algebraical sum of the tetanic functional currents of all the muscles exerted, although such an explanation only became very probable by the exclusion of certain other experiments designed to elucidate the matter.[1] But the current could never be demonstrated under the most favourable conditions of abduction, viz., by the application of the galvanometer wires to individual groups of muscles.[2]

The question whether the diminution of the excitatory wave only occurs in excised muscles as a result of death changes, could, of course, only be settled by experiments on living human beings. And since the manifold disturbances inseparable from the method of experiment rendered the tetanic functional current almost useless for this investigation, I undertook to examine the *phasic* current in the muscles of the fore-arm.[3] I found that the same relationship held for the muscles of man as had before been shown to exist in the case of the frog. The first phase is an atterminal current in which the region of the nervous equator—about 10 cm. below the elbow—becomes negative in comparison with the two ends; the second phase is abterminal, *i.e.*, the ends of the muscles become negative in comparison with the equator (Fig. 7). But in the perfectly normal muscles of man the second phase was *not* weaker than the first—a relation which was constant in the excised muscles of the frog. And hence we may conclude that in absolutely normal muscles the excitatory wave does not diminish in intensity. These experiments, which constitute the first regular examination of muscular action in living man, further taught approximately the rate of propagation of the excitatory wave in human muscles, viz., from 10 to 13 metres per second.

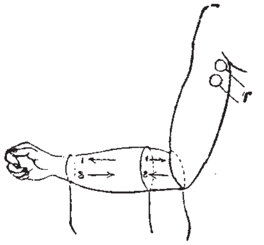

FIG. 7.

### *The Absence of the Functional Current when none of the above Conditions of Electrical Inequality exist in Muscle*

If an uninjured, currentless muscle be thrown into the active condition by a stimulus affecting its whole mass at once, it never exhibits any functional current,[4] whether the stimulus be single or tetanic. The explanation of this is obvious. In such a totally excited muscle the whole substance passes at the same moment into the same degree of excitation; and, hence, is nowhere the opportunity given for the contact of excited with non-excited or imperfectly excited tissue.

If, on the other hand, the muscle possesses an artificial transverse section with the associated boundary current, then indeed a levelling or equalising functional current arises on total excitation and diminishes the current of injury.[5]

When muscles are tetanised through their nerves, functional currents only appear where the excitatory wave has not the same intensity throughout the tetanised mass. Hence in man, whose muscles when under absolutely normal conditions exhibit no diminution or decrement of wave, it is impossible to demonstrate a tetanic functional current. I have, indeed, when using very powerful and fatiguing stimulation, now and then succeeded in getting indications of such a decremental functional current, but from some cause or other, we cannot depend upon this experiment to lead to a constant result, perhaps for the reason that the conductivity of human muscles is but slightly hampered by fatigue, or possibly because the collateral effects of stimulation mar the experiment.[6] I may be allowed to remark here that certain experiments now in course of publication show very clearly that stimulation of human muscles causes a secretory cutaneous current directed from without inwards. This current is the true cause of the negative potential exhibited by the voluntarily contracted muscles of one limb when compared with the opposite but unexerted limb, and is therefore the current which du Bois-Reymond took for the muscular functional current of man.[1]

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[1] Du Bois-Reymond, *loc. cit.*, 1873-76.

[2] "Arch. f. d. ges. Physiol.," xvi. p. 236.

[3] *Ibid.*, p. 239.

[1] Du Bois-Reymond, "Untersuchungen," ii., Abth. 2, p. 267.

[2] "Arch. f. d. ges. Physiol.," xvi., p. 257, 1877.

[3] *Ibid.*, xvi., p. 410, 1878.

[4] "Arch. f. d. ges. Physiol.," xvi., p. 203, 1877.

[5] *Ibid.*, xv., p. 238; xvi., p. 203, *et seq.*, 1877.

[6] *Ibid.*, xvi., p. 416, 1878.

## B.—NERVES

### *The Functional Current of Nerves remote from all Transverse Sections*

In the nerves of the frog, according to Helmholtz, excitatory waves are propagated at the rate of twenty-eight metres per second. Hence, if the two ends of a galvanometer circuit were laid upon two points of a nerve a functional current should be manifest on stimulation of the nerve, and should consist of two phases according as the excitatory wave was passing one or the other of the electrodes. Nevertheless the functional current of nerves, owing doubtless to its exceedingly fleeting character, has hitherto escaped detection.[2] Since the excitatory wave of nerves does not diminish in its course, it is to be expected that the two phases of the nervous functional current will be equal; and hence also it is that in tetanic stimulation, where we have to do with the algebraical sum of these two equal and opposite phases, we obtain no functional current whatever in uninjured nerves.

### *The Functional Current of Nerves at a Transverse Section*

The functional current of nerves bounded by an artificial transverse section was discovered by du Bois-Reymond; it is an equalising current, and consists, therefore, in a diminution of the constant demarcation current. Du Bois-Reymond only found this current in nerves tetanically stimulated, but Bernstein, by means of his apparatus already referred to, succeeded in demonstrating its presence in the case of single excitatory waves.[3] If the poles of the galvanometer circuit are applied, one to the artificial cross-section, and the other to a point in the longitudinal surface, the diminution of the demarcation current occurs in the instant that the excitatory wave passes the latter, or longitudinal pole. By altering the position of this pole, the progress and the course in time of the excitatory wave may be examined. The rate of progression so deduced was found to agree with that determined in other experiments by varying the distance between the point of the nerve at which a stimulus was applied and the fixed point at which the result of stimulation was manifested, viz., the dependent muscle, or the pole applied to an artificial cross-section. And this similarity of result established the identity of the process occurring during excitation, and the wave of negative deflection.[4] The way in which the wave comports itself on approaching the artificial cross-section will be explained below.

### *The Functional Current of Polarised Nerves: the Polarisational Increment of Excitation*

In 1866 Bernstein found[5] that the electrotonic currents of nerve, on stimulation of the nerve, suffer diminution like the demarcation-currents. As a disciple of the molecular theory he explained this phenomenon in the following way: Since the electrotonic currents depend upon an altered arrangement of the molecules, and since the force of each molecule diminishes on stimulation of the nerve, therefore the electrotonic currents must also be lessened during excitation. And so the new phenomenon seemed to be completely covered by the molecular theory. In my view, however, the electrotonic currents are merely offsets diverted from the main polarising current owing to the internal polarisation of the nerve itself. Since these offsets could not be supposed to be modified during excitation, I concluded that every apparent diminution depended upon a functional current which arises owing to the polarised condition of the nerve, and which is opposite to the polarising current in direction. I assumed, as the cause of this functional current, that the excitatory wave failed of maintaining its magnitude while passing through the polarised portions of nerve; it increased as it reached more positively or less negatively polarised areas, and diminished under the opposite conditions. This is called the doctrine of the "polarisational increment of excitation,"[1] and it is clearly competent to explain Bernstein's observations.

If this assumption be reasonable, the excitatory condition travelling along the nerve should be most intense at the anode of the polarising current, and least intense at the cathode; and hence there should be present in the intrapolar region a powerful functional current of like-direction with the polarising current and reinforcing it. Such an intrapolar current I did, in fact, discover to be constantly present;[2] though afterwards it appeared that a similar observation had previously been made by Grünhagen, by whom, however, the current was otherwise explained as the effect of a diminished resistance in the nerve during excitation, leading to an increase in the polarising current.[3] Before I had any knowledge of this early observation of Grünhagen, the probability of the explanation which he assigned to it had been tested by me, and numerous indications had been found that the intrapolar increase of current was indeed an electromotive phenomenon and not due to a diminished resistance.[4] But later I was enabled to settle the question in the most direct manner, by the discovery that the transverse resistance of nerves is *not* diminished during excitation—excitation having in general no manner of influence upon the resistance offered by the nerve.[5]

### *Further Physiological Support of the Doctrine of Polarisational Increment*

In order to grasp the doctrine of polarisational increment, let us regard the axis *n n'* in Fig. 5 as representing a nerve, the conditions of polarisation of which are indicated by the vertical ordinates, positive polarisation being exceptionally represented by descending lines, and negative by ascending lines. With these ordinates we can trace out the polarisation curve, *n* K *i* A *n'* (already spoken of in describing Fig. 5, which see), the lowest point of which corresponds to the anode, and the highest to the cathode. Let us now suppose a ball, *e*, devoid of friction, and travelling through space with a certain horizontal initial velocity, to be set rolling along this curve. The *vis viva* of the ball will then represent the magnitude of excitation. It is at once evident that the initial velocity is increased in the part of the curve below the line *n n'*, *i.e.*, in the anelectrotonic region, but is diminished in the upper portions of the curve, *i.e.*, in the catelectrotonic region. If the initial velocity is too small, the ball will not be able to reach the summit of the catelectrotonic portion of the curve, or, in other words, the excitation becomes dissipated in the corresponding region of nerve, and never succeeds in passing the cathode. Moreover, if the ball, with a certain initial velocity, were to be set going at some point of the inferior (anelectrotonic) portion of the curve, it would reach the outlying parts beyond the polarised region with a diminished velocity; while, if it were set going upon a part of the curve (catelectrotonic) superior to the line *n n'*, it would reach the outlying parts with an increased velocity.

All these deductions from the doctrine under discussion have been verified, in part by already established facts and in part by recent observations. The experiments by Eckhard and Pflüger have shown that a certain stimulus applied to a nerve produces a greater effect in the catelectrotonic region than in the anelectrotonic. And it is clear that these phenomena are as intelligible under my theory as under the assumption usually made to explain them, viz., that the irritability of the nerve itself is diminished during anelectrotonus and increased during catelectrotonus.[6]

Moreover, certain facts are known which seem to imply that, with a sufficient degree of polarisation, or with a sufficiently slight stimulus, the excitatory wave becomes blocked at the cathode.[7] If to this we add that excitation does not indefinitely increase with the stimulus, but soon reaches a maximum, we may further conclude that, under certain conditions, a diminution of excitation must take place even during the passage of the wave through the anodic area.[8]

In the last place it is to be noticed, that the artificial section of a nerve induces a negative polarisation or catelectrotonus of the fibres in the neighbourhood of the section, owing to the extension of the demarcation-current along the nerve.[1]

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[1] These experiments have been recently published; cf. Hermann and Zuchsinger, "Arch. f. d. ges. Physiol.," xvii. p. 310, 1878.

[2] I have succeeded in detecting these currents by extending the rate of propagation in the nerve by cold; and by using a bundle of four or six nerves together. Cf. "Arch. f. d. ges. Physiol.," xviii., p. 574, 1878.

[3] J. Bernstein, *loc. cit.*

[4] The new experiments referred to in the last note confirm this indirect conclusion in a more direct manner.

[5] J. Bernstein, "Arch. f. Anat. u. Physiol." p. 596, 1866.

[1] "Arch. f. d. ges. Physiol.," vi., p. 359, 1872; vii., p. 323, 1873.

[2] *Ibid.*, vi., p. 560, 1872; vii., p. 355, 1873; x., p. 215, 1875.

[3] Grünhagen, "Zeitsch. f. rat. Med." (3), xxxvi., p. 132, 1869.

[4] "Arch. f. d. ges. Physiol.," x., p. 215, 1875.

[5] *Ibid.*, xii., p. 151, 1875.

[6] *Ibid.*, vii., pp. 325, 497, 1873.

[7] *Ibid.*, vii., p. 354, 1873; x., p. 226, 1875.

[8] *Ibid.*, vii., p. 361, 1873.

By this electrotonic extension we can explain—or for the most part explain—the so-called "weak currents" of the longitudinal section.[2] A stimulus applied to the nerve near the line of section, according to the law of polarisational increment, should have a greater effect than when applied to points more remote, and this experiment shows to be the case. Finally, an excitatory wave travelling along the nerve towards the cut end of it must, according to the same law, gradually diminish before it disappears entirely in the area of section itself.

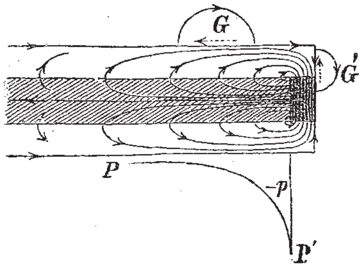

FIG. 8.

### V. CONCLUDING REMARKS

The whole of the electrical phenomena of muscle and nerve, therefore, may be readily deduced from a few very simple propositions. Irritable protoplasm responds both to destructive and to exciting influences by an electromotive sign. The altered substance takes on a negative potential with respect to the unaltered. This, together with the doctrines of internal transverse polarisation and of the polarisational increment of excitation, appears fully competent to explain all the facts hitherto observed.

That these fundamental doctrines have the closest reference to the whole life of irritable tissues no one will be disposed to doubt. Yet much examination will be needed to disclose the exact nature of the interdependence.

Although it must now be confessed that the theories which were based upon facts discovered more than thirty years ago, have failed to withstand the criticism of a wider experience, the domain of animal electricity has not lost, but rather gained in interest. And the services of the man who not only discovered this region of physiology, but created the means of conquering it, and who made himself master of its most important fundamental features, are in no danger of becoming dimmed in our estimation by the theoretical changes we have been compelled to accept.

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## BAROMETRIC PRESSURE

IN a work of great importance,[3] recently published by Prof. Bert, on the physiological effects of barometrical pressure, the author sums up the conclusions to be drawn from his researches as follows:—

A. The diminution of barometric pressure acts on living beings only by diminishing the tension of the oxygen in the air which they breathe, in the blood which animates their tissues (*anoxytienne* of M. Jourdanet), and by thus exposing them to the dangers of asphyxia.

B. The increase of barometric pressure acts only by increasing the tension of the oxygen in the air and the blood. Up to about three atmospheres this increase of tension gives rise to intra-organic oxidations a little more active. Beyond five atmospheres the oxidations diminish in intensity, probably change in their nature, and, when the pressure rises sufficiently, are completely arrested. It follows that all living beings, aërial or aquatic, animal or vegetable, complex or mono-cellular—that all the anatomical elements, isolated (blood-globules, &c.) or grouped in tissues, perish more or less rapidly in air sufficiently compressed. This rule appears only to suffer exception for the reproductive corpuscles of some microscopic beings. For the higher animals death is preceded by tonic and clonic convulsions of extreme violence. Among vertebrates the rapid accidents due to the too great tension of oxygen only commence to manifest themselves at the moment when the hæmoglobin, being saturated with oxygen, that gas enters into the state of simple dissolution in contact with the tissues.

C. Diastases, poisons, and true virus resist the action of oxygen at high tension.

D. The inconvenient effects of diminution of pressure may be efficaciously combatted by the respiration of an air sufficiently rich in oxygen to maintain the tension of that gas at its normal value (20·9). Those of the increase of pressure may be combatted by employing air sufficiently poor in oxygen to arrive at the same result.

E. Generally the favourable or noxious gases (oxygen, carbonic acid, &c.) act only on living beings in accordance with the tension which they possess in the surrounding atmosphere, a tension which is measured by multiplying their centesimal proportion by the barometric pressure; the increase of one of the factors may be compensated by the diminution of the other.

F. When animals possess reservoirs of air either completely closed (swimming bladder of acanthopterygians, &c.) or in communication with the air during decompression alone (swimming vessel of the Cyprini, intestines of aërial vertebrates, &c.), or in communication with the air during both compression and decompression, but by very small orifices (lungs of aërial vertebrates, &c.), the diminution or increase of pressure may have physico-mechanical effects.

G. Sudden decompression from several atmospheres has only the effect (except for some cases comprised under conclusion F) of allowing to return to the free state the nitrogen which was, under favour of pressure, dissolved in the blood and the tissues.

H. The beings actually existing in a wild state on the surface of the globe are accommodated to the degree of oxygenated tension under which they live; all diminution, all increase, appears to be unfavourable to them when they are in a state of health. Therapeutics might make something out of these modifications in various patholgical conditions.

I. Barometric pressure and the proportion per cent. of oxygen have not always been the same on our globe. The tension of that gas has apparently been, and will without doubt continue to go on, diminishing. There is here a factor which we have not yet taken into account in biogenetic speculations. The power of reaction against these various modifications leads to the supposition that microscopic beings must have appeared first, and that they will be extinguished by the insufficient tension of oxygen.

K. It is inaccurate to teach, as is ordinarily done, that vegetables must have appeared in the earth before animals, in order to purify the air of the great quantity of $CO_2$ which it contained. In fact, germination, even that of mildew, does not take place in air sufficiently charged with $CO_2$ to be fatal to warm-blooded animals. It is quite as inaccurate, as I have observed long ago, to explain the anteriority of reptiles with warm-blooded animals by the impurity of the air tainted with too much $CO_2$; reptiles, in fact, are more injured by this gas than birds, and still more so than mammals.

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## SCIENTIFIC SERIALS

THE *Sitzungsberichte* of the Vienna Imperial Academy of Sciences (Natural History Section, vol. lxxvi. parts 1–5, and vol. lxxvii. parts 1–4) contain the following more important papers:—Addenda to our knowledge of annelids, by Dr. Aug. v. Mojsisovics.—On the orthoptera of the Senegal River, by Dr. H. Kraus.—On the fauna of the Cypris slates of the Eger tertiary strata, by O. Novák.—On the natural history of glimmer, by G. Tschermak.—Researches on cystolithes and some similar formations in the vegetable kingdom, by K. Richter.—On the genesis of salt deposits, particularly of those in western North America, by F. Posepny.—On the fresh-water fish of South-Eastern Brazil, by Dr. F. Steindachner.—On the "Salse di Sassuolo"

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[1] "Arch. f. d. ges. Physiol.," vii., p. 363, 1873. This polarisation, of course, still occurs even when the demarcation-current is not abducted, or when the abducted portion is counterbalanced by an opposite current. In the latter case, according to Bosscha's law, the nerve behaves just as if no abducting circuit were applied to it. "Arch. f. d. ges. Physiol.," ix., p. 29, 1874; x., p. 237, 1875.

[2] In Fig. 8 the core of the nerve-fibre is obliquely shaded. Even in the absence of polarisation of the core the boundary current would become distributed after the manner shown in the figure, and would pass into the galvanometer circuits G and G' as the so-called weak longitudinal and transverse currents of du Bois-Reymond. But, with polarisation, the extension along the core is very much greater than without it, and at the same time the polarisational curve $pp'$ is produced.

[3] "La Pression Barométrique; Recherches de Physiologie Experimentale." Par Paul Bert, Professor à la Faculté des Sciences de Paris. (Paris: G. Masson. 1878.)